



## ON A NEW MANIRAPTORAN DINOSAUR (THEROPODA) FROM THE UPPER CRETACEOUS OF NEUQUÉN, PATAGONIA, ARGENTINA <sup>1</sup>

(With 41 figures)

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**ABSTRACT:** The “Futalognko” site, situated at the margins of the Los Barreales lake about 90 km northwest of Neuquén city (Patagonia), revealed several new dinosaur specimens, all from the Portezuelo Formation (Turonian-Early Coniacian). Among those are the remains of new theropod dinosaur referable to a new species of the maniraptoran *Unenlagia*, *Unenlagia paynemili* n. sp. The material is represented by a pubis, humerus, ilium, and a dorsal vertebra, plus a pedal phalanx and a claw that tentatively referred to this new species. It shares with *Unenlagia comahuensis* a posteriorly oriented distal end of the pubis that shows a convex anterior margin and differs by possessing more gracile bones, angle between the anterior rim of the deltopectoral crest and the humerus shaft more closed, the presence of a small anterior process on the distal end of pubis, and the distal end of the postacetabular blade of ilium broader and rounded, with a shallower *brevis fossa*.

**Key words:** Dinosauria, Maniraptora, Portezuelo Formation, Patagonia, Argentina

**RESUMO:** Sobre um novo dinossauro Maniraptora (Theropoda) do Cretáceo Superior de Neuquén, Patagônia, Argentina.

Novos materiais de dinossauros, todos procedentes da Formação Portezuelo (Turoniano-Coniaciano Inferior), foram encontrados nos últimos anos na localidade denominada de “Futalognko”, situada às margens do lago Barreales a cerca de 90 km noroeste da cidade de Neuquén (Patagonia). Entre estes se destaca uma nova espécie do maniraptora *Unenlagia*, denominado aqui de *Unenlagia paynemili* n. sp. O material é representado pelo úmero, púbis, ílio e uma vértebra dorsal, além de uma falange e uma ungueal, atribuídos por tentativa a essa nova espécie. A principal característica compartilhada com *Unenlagia comahuensis* é a margem anterior convexa do púbis, com a parte distal orientada posteriormente. As principais diferenças observadas na nova espécie são os ossos mais gráteis, o ângulo entre a crista deltopeitoral e eixo do úmero mais fechado, a presença de uma projeção anterior no púbis, e a porção pós-acetabular do ílio mais larga e arredondada, com a *brevis fossa* mais rasa.

**Palavras-chave:** Dinosauria, Maniraptora, Formação Portezuelo, Patagônia, Argentina

### INTRODUCTION

In 2000, the team of the National University of Comahue has discovered an important fossil deposit about 90km northwest of the Neuquén city (Patagonia), Argentina (CALVO *et al.*, 2002b). Called the Futalognko site, this quarry is placed at Costa Dinosaurio Locality, northern coast of the Barreales lake. Due to the richness of fossils a new Paleontological Center of the National University of Comahue was built there. Today, this complex is named Barreales Lake Paleontological Center

(CePaLB) and consists the first permanent educational paleontological site in South America fully dedicated to field research in vertebrate paleontology.

The fossiliferous beds of the Futalognko site are from the Turonian- Early Coniacian Portezuelo Formation of the Rio Neuquén Group (LEANZA & HUGO, 2001) and yielded several important vertebrate fossils. Among those are titanosaurid sauropods (CALVO *et al.*, 2001, CALVO & GRILL, 2003), new material from the theropod *Megaraptor namunhuaiquii* Novas, 1998 (CALVO *et al.*, 2002a;

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PORFIRI & CALVO, 2003), theropod teeth (POBLETE & CALVO, 2003; VERALLI & CALVO, 2003) ornithopods (PORFIRI & CALVO, 2002), turtles, osteichthyan fishes (GALLO, CALVO & KELLNER, 2003), crocodylomorphs, pterosaurs (KELLNER *et al.*, 2004), and plants (PRÁMPARO *et al.*, 2003).

During the field season of 2002, another interesting material was recovered from this site. It consists of isolated remains, including the left humerus and left pubis that share several features with the maniraptoran *Unenlagia comahuensis* Novas & Puerta, 1997 (CALVO, PORFIRI & KELLNER, 2003). The latter was found at the Sierra del Portezuelo, about 50km south of the Futalognko site (NOVAS & PUERTA, 1997). In 2003, one dorsal vertebra and the posterior end of one right ilium, also sharing several features with *Unenlagia comahuensis*, were recovered from that site. The purpose of this paper is to report this material, which is referred to a new species of *Unenlagia* (*U. paynemili* n.sp.). An isolated phalanx and ungual, also recovered from the site, are tentatively referred to the new taxon, which is described here.

#### GEOLOGICAL SETTING

The Neuquén Basin of western Argentina has deposits ranging from the Upper Triassic to the Tertiary. These deposits include a sequence of marine and continental strata, including the Neuquén Group, which is composed of sediments formed in a continental, fluvial environment that range from Albian to Campanian age (ULIANA & DELLAPE, 1981; LEGARRETA & GULISANO, 1989; CALVO, 1991; CALVO & SALGADO, 1995).

The material of the new species, *Unenlagia paynemili* n.sp., comes from continental deposits from the top of the Portezuelo Formation, Río Neuquén Subgroup, Neuquén Group (CAZAU & ULIANA, 1973; LEANZA, 1999). The Río Neuquén Subgroup is composed of two formations, at the base the Portezuelo and at the top the Plottier formations. The Portezuelo Formation is characterized by yellowish sandstones, red and green claystones with a poor participation of conglomerates, which have been interpreted as Turonian - Early Coniacian (LEANZA & HUGO, 2001). The depositional environment is interpreted as a meandering river system that runs over a flattened area by an exuberant vegetation in humid climate conditions (SÁNCHEZ *et al.*, 2003). Fossils were recovered from a fine conglomerate and are mostly unarticulated.

#### SYSTEMATIC PALEONTOLOGY

Theropoda Marsh, 1881  
 Coelurosauria Gauthier, 1986  
 Maniraptora Gauthier, 1986  
*Unenlagia* Novas & Puerta, 1997

Type-species – *Unenlagia comahuensis* Novas & Puerta, 1997

*Unenlagia paynemili* n.sp.

Etymology – In honor to Maximino Paynemil, the chief of the Paynemil Indian community that lives in the region of Loma de La Lata, where the Futalognko site is situated.

Holotype – Left humerus and left pubis, regarded as belonging to the same individual, housed at the Museo de Geología y Paleontología de la Universidad Nacional del Comahue under the number MUCPv-349.

Referred specimens – A dorsal vertebra (MUCPv-416) and the posterior end of a right ilium (MUCPv-409). Tentatively, a pedal phalanx (MUCPv-415) and a pedal claw (MUCPv-343) are also referred to this species.

Locality and horizon – Futalognko site at the Centro Paleontológico Lago Barreales situated about 90km northwest of the Neuquén city, Neuquén province, Patagonia, Argentina; Portezuelo Formation (Turonian-Early Coniacian), Río Neuquén Group.

Diagnosis – Species of *Unenlagia* distinguishable from *Unenlagia comahuensis* by possessing more gracile bones, the angle between the anterior rim of the deltopectoral crest and the humerus shaft about 116° (opposed to 140° of *Unenlagia comahuensis*), a small anterior process on the distal end of pubis, and the distal end of the postacetabular blade of ilium broader and rounded, and a shallower brevis fossa.

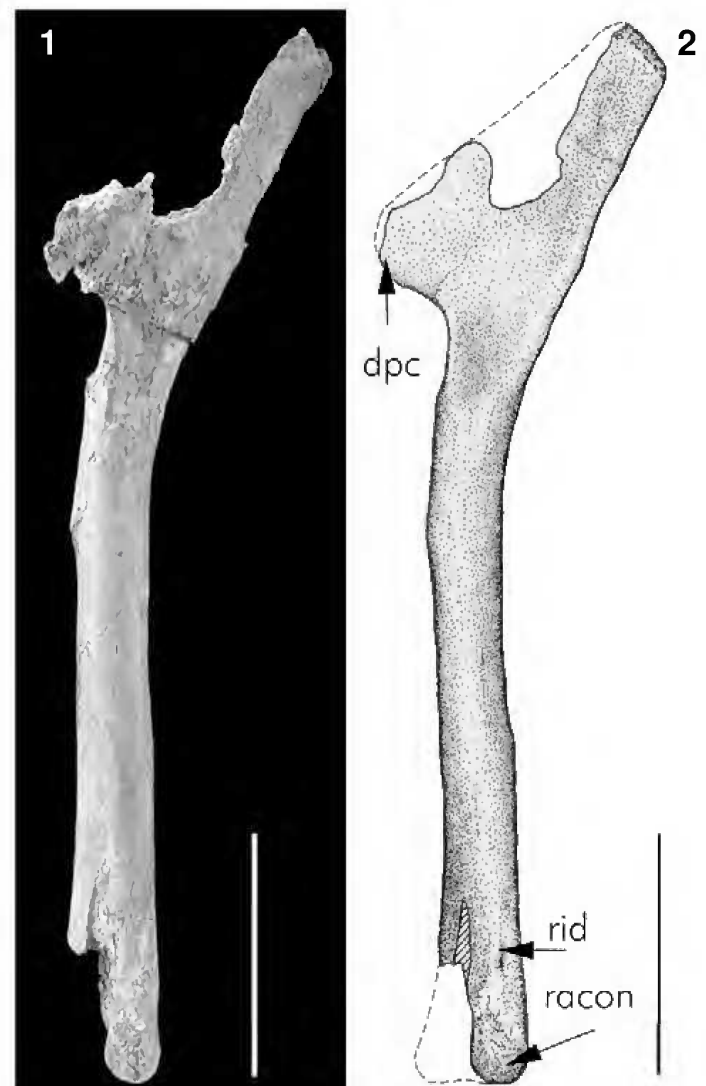
#### DESCRIPTIONS AND COMPARISONS

Since 2002 a quarry map of the Futalognko site showing the relation of all collected fossil remains is being made, including the elements attributed to *Unenlagia paynemili* n.sp., which were found isolated. The pubis and the humerus were lying about two and half meters from each other (close to the remains of the giant sauropod) and are regarded as belonging to the same individual due to their proximity in the quarry and similarity in size when compared to the material of the larger *Unenlagia comahuensis*. Furthermore, both bones have a

distinct brownish color, different from the other sauropod and theropod elements (*e.g.*, *Megaraptor namunhuaiquii*) collected at the site. Although the size of the ilium (and the bone color) is also compatible with the humerus and pubis, it was found more distant (ca. 23 meters from the pubis) and is regarded as belonging to a different individual. The last element attributed to *Unenlagia paynemili* n.sp. is an incomplete dorsal vertebrae that belongs to a proportionally larger individual (also larger than the type material of *Unenlagia comahuensis*) and was found in 2003 by surface collecting (probably washed out from the quarry during the flooding of the Barreales lake). Two more bones are described and are tentatively referred to *Unenlagia paynemili* n.sp.: a pedal phalanx and an ungual, also found isolated (respectively 5 and 12.5 meters from the pubis). Except for the humerus and pubis, all remaining specimens are numbered separately.

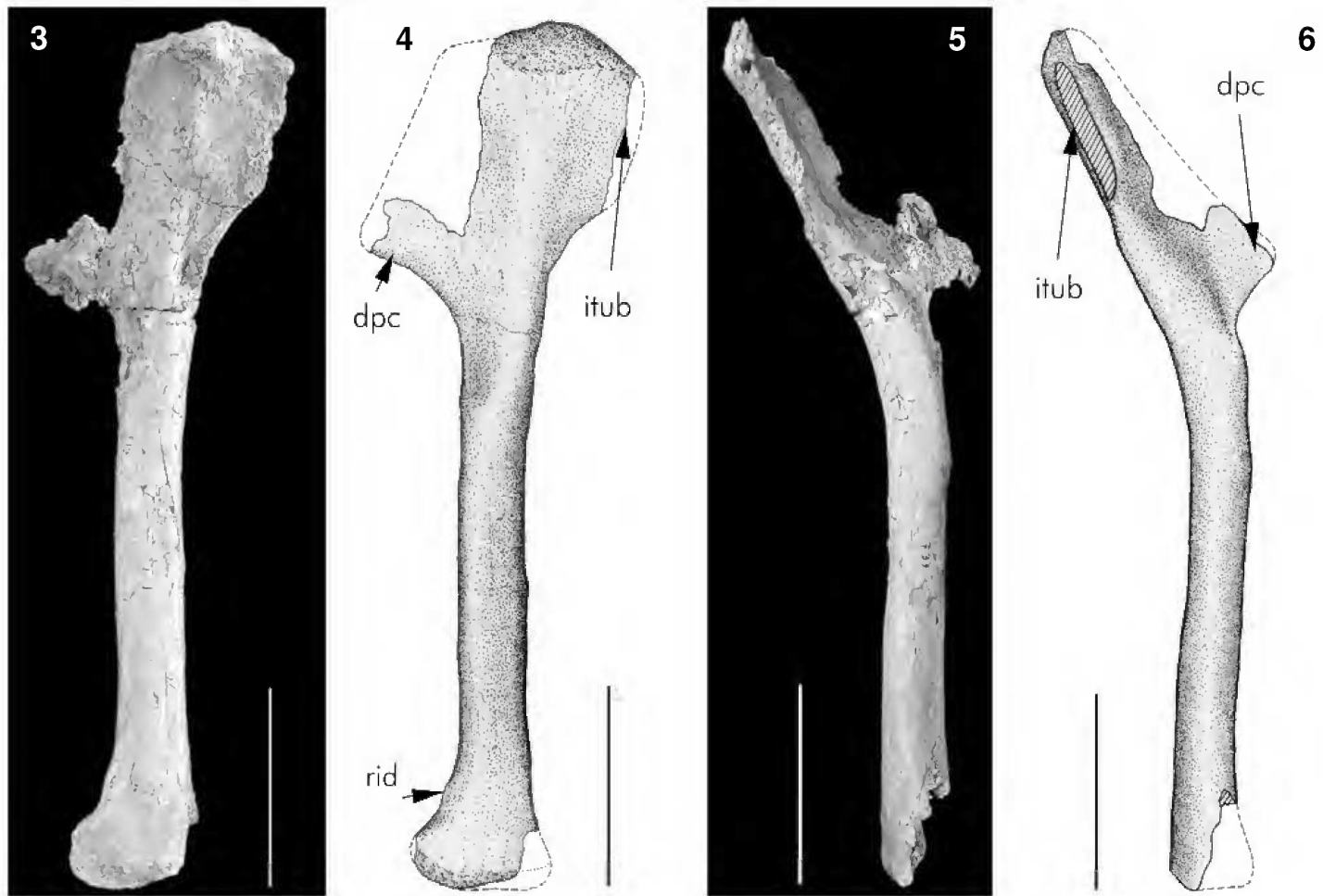
The humerus (MUCPv-349) belongs to the left side and except for some parts of the proximal and distal articulations is complete with a total length of 217mm (Figs.1-10). It is a long and slender pneumatic bone, with the thickness of the cortex around 2mm. The proximal part is flattened anteroposteriorly. The deltopectoral crest is expanded and restricted to the proximal third of the humerus, a condition common to other maniraptorans. It is thin and inclined about 116 degrees relative to the shaft. The preserved part of the internal tuberosity is anteroposteriorly compressed and longitudinally elongated as in *Unenlagia comahuensis*, *Deinonychus antirrhopus* Ostrom 1969, *Archaeopteryx lithographica* Meyer 1860, and some other maniraptorans (OSTROM, 1969a, b; WELLNHOFER, 1974; 1993; NOVAS & PUERTA, 1997). The shaft is essentially straight and long differing from the bowed condition present in some maniraptorans like *Deinonychus antirrhopus* (OSTROM, 1969b). It is slightly compressed anteroposteriorly with an oval cross section over most its length (middle part = 17.5 x 14mm) and gets more triangular closer to the distal articulation. A blunt longitudinal ridge (length 20mm) is observed above the radial condyle (partially preserved) at the dorsal margin close to the posterior surface (Figs.1-4, 7, 8). Overall, the humerus of *Unenlagia paynemili* n.sp. is similar to the one of *Unenlagia comahuensis* (Figs.9-10). Both have the proximal part, that includes the deltopectoral crest, strongly deflected relative to the shaft. The deltopectoral crest in those taxa is quadrangular in anterior view, similar to oviraptorids (BARSBOLD, MARYANSKA & OSMÓLSKA, 1990) and most dromeosaurids (OSTROM, 1969a, b), but differs

from the distinct and long deltopectoral crest of alvarezsaurids (*e.g.*, NOVAS, 1996) and the less pronounced condition reported in *Archaeopteryx lithographica* (WELLNHOFER, 1974; 1993) and in the Ornithomimosauria (BARSBOLD & OSMÓLSKA, 1990). The humerus of *Unenlagia paynemili* n.sp. differs from *Unenlagia comahuensis* mainly by being about 20% smaller and a more gracile element. Furthermore, the angle between the ventral margin of the deltopectoral crest in the new species is 116° while in *Unenlagia comahuensis* it is wider, about 140° (Figs.9-10). The latter also shows a developed blunt ridge on the dorsal margin posterior to the deltopectoral crest that is not observed in the new species (Figs.9-10).



*Unenlagia paynemili* n.sp., left humerus (MUCPv-349) in dorsal view – fig.1- picture; fig.2- drawing. (dpc) deltopectoral crest, (itub) internal tuberosity, (rad) radial condyle, (rid) ridge. Scale bars = 50mm.





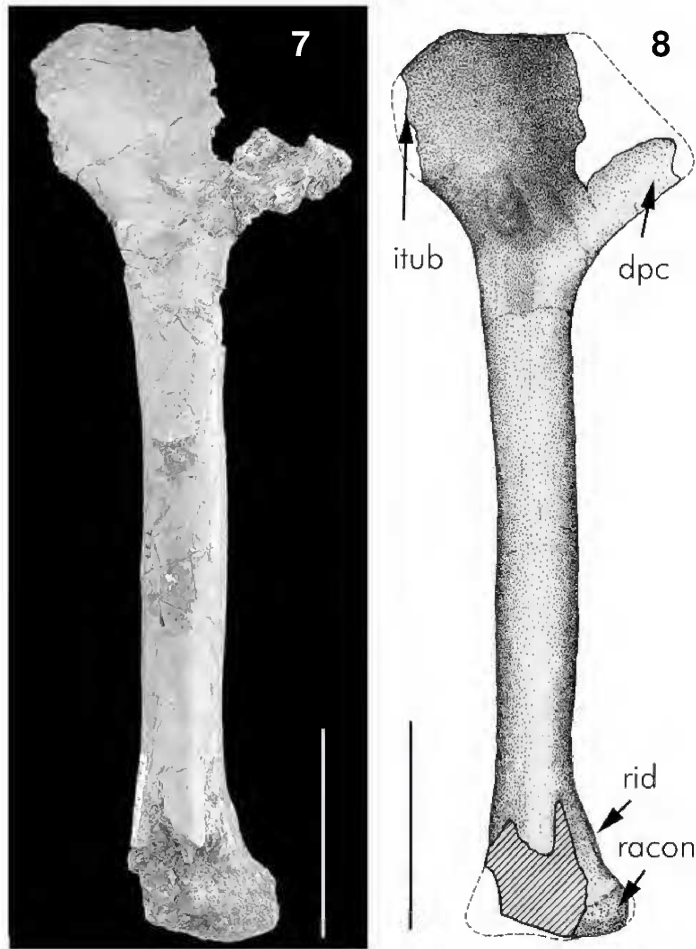
*Unenlagia paynemili* n.sp., left humerus (MUCPv-349) – fig.3- picture, posterior view; fig.4- drawing, posterior view; fig.5- picture, ventral view; fig.6- drawing, ventral view. (dpc) delto pectoral crest, (itub) internal tuberosity, (rid) ridge. Scale bars = 50mm.

The left pubis (MUCPv-349) of *Unenlagia paynemili* n.sp. is almost complete (length: 267mm) while the right one is represented only by a thin layer of bone at the tip of the distal half, forming the pubic boot (Figs.11-19). Overall, the pubis is a slender and comparatively thin bone, with an anteroposteriorly expanded proximal end that is slightly displaced medially (anterior view). In proximal view, the iliac articulation is slightly concave, long and narrow. The shaft has a convex anterior surface, with the distal part directed posteroventrally. In anteroposterior view, the lateral margin is sigmoidal, with the proximal half concave and the distal half convex. The distal end is expanded anteroposteriorly, with both pubes fusing in the midline forming a pubic boot, and showing a small anterior projection (Figs.11-16). The pubic apron is deflected posteriorly and extends for about 135mm, reaching half the public

shaft (Figs.13-18). Apparently this flange is too narrow to meet at the midline with the opposite element. Except for the proximal region, most of the pubic flange extends medially from the anterior margin of the shaft.

Although no complete ilium is available for *Unenlagia paynemili* n.sp., the comparisons with other maniraptorans, particularly *Unenlagia comahuensis* indicate that the pubes is positioned vertically. The pubic apron of the new form is extended for about half of the public shaft like in most maniraptorans but differing from the smaller pubic apron diagnostic of the Avialae (NORELL, CLARK & MAKOVICKY, 2001). Contrary to some other maniraptorans (e.g., *Velociraptor* Osborn, 1924), the opposite flange forming the pubic apron apparently does not meet in the midline, a condition also reported in *Unenlagia comahuensis* (NOVAS & PUERTA, 1997).





*Unenlagia paynemili* n.sp., left humerus (MUCPv-349) - fig.7-picture; fig.8- drawing. (dpc) delto pectoral crest; (itub) internal tuberosity; (rad) radial condyle; (rid) ridge. Scale bars = 50mm.

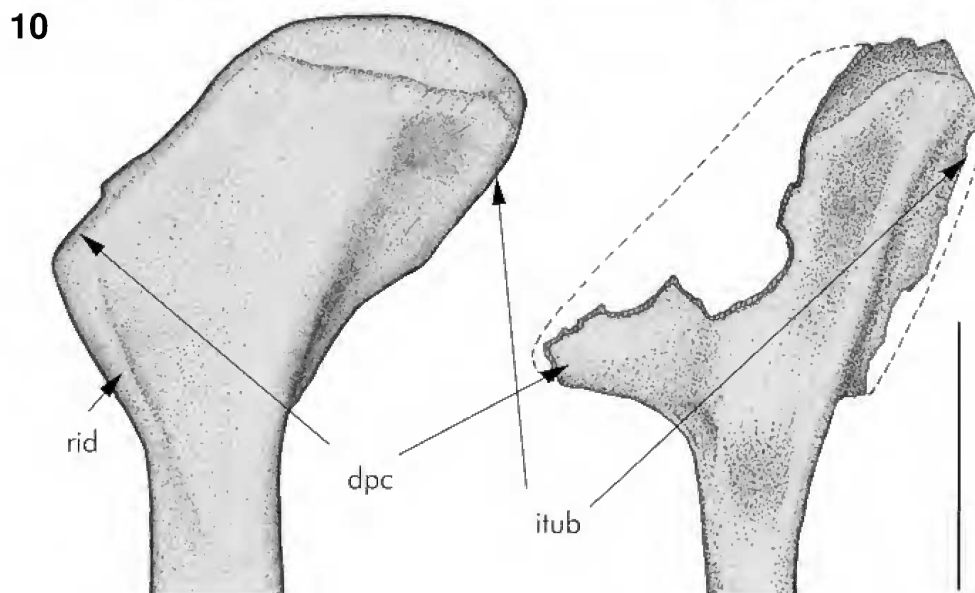
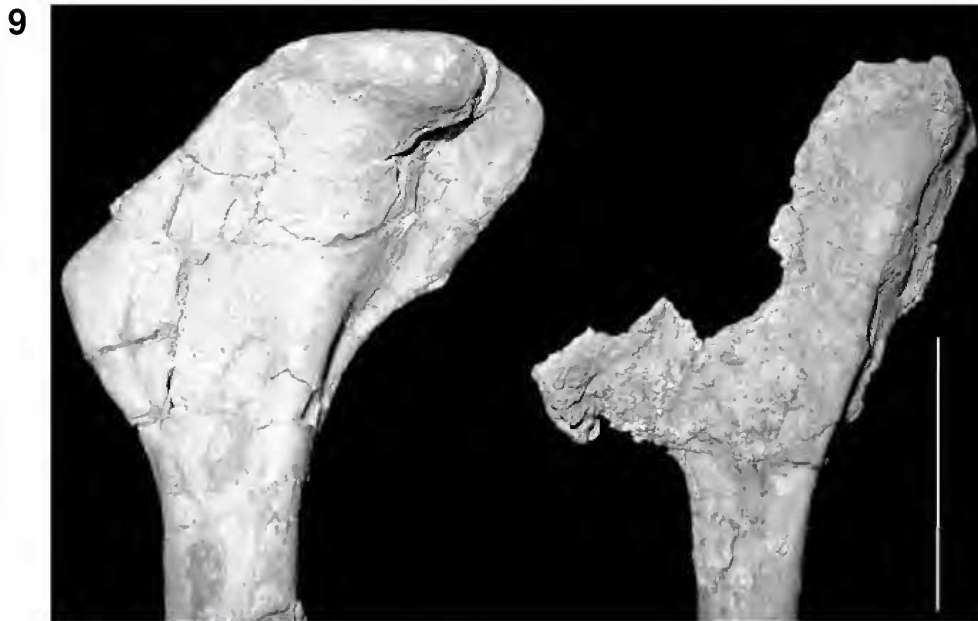
The comparisons of the pubes of *Unenlagia paynemili* n.sp. with other maniraptorans show that it is more similar to *Unenlagia comahuensis*, both sharing at least one feature: the posteriorly oriented distal end of the pubis that shows a convex anterior margin (Figs.20-21). Although NOVAS & PUERTA (1997) reconstructed the pubis of *Unenlagia comahuensis* in a straight fashion in lateral view, a closer examination of the holotype indicates that the pubis (particularly the left one) had the distal part directed posteriorly as in *Unenlagia paynemili* n.sp., this character is considered a synapomorphy of *Unenlagia*. This feature differs from the straight pubes found in most other theropods and from the anteriorly curved distal pubic end of the oviraptorids (BARSBOLD, MARYANSKA & OSMÓLSKA, 1990).

The main difference between the pubes of *U. paynemili* n.sp. and *U. comahuensis* is the presence of an anterior component in the pubic boot in the new

species absent in the latter. More basal theropods such as *Carnotaurus* Bonaparte, 1985 (BONAPARTE, NOVAS & CORIA, 1990), *Pycnonemosaurus* Kellner & Campos, 2002 (KELLNER & CAMPOS, 2002), *Sinraptor* Currie & Zhao, 1993 (CURRIE & ZHAO, 1993) and many coelurosaurs like the Oviraptorosauria (BARSBOLD, MARYANSKA & OSMÓLSKA, 1990) have the anterior portion of the pubes more developed. Other maniraptorans like *Velociraptor* also show a small anterior extension of the pubic boot (NORELL & MAKOVICKY, 1999) but differ from *Unenlagia paynemili* n.sp. by being dorsoventrally expanded.

In posterior view, the shaft is bowed at the third distal end as in *Unenlagia comahuensis*, differing from other maniraptorans where the lateral margin is bowed more proximally like *Velociraptor mongolensis* Osborn, 1924 (NORELL & MAKOVICKY, 1999); or straight like *Achillobator giganticus* Perle, Norell & Clark, 1999 (PERLE, NORELL & CLARK, 1999); *Tyrannosaurus rex* Osborn, 1905 (OSBORN, 1905; BROCHU, 2003); *Avimimus portentosus* Kurzanov, 1981; Coelurosaurs indet. (MARTILL *et al.*, 2000). This character is just present in *Unenlagia comahuensis* and *Unenlagia paynemili* n.sp. and it might be another synapomorphy uniting those taxa.

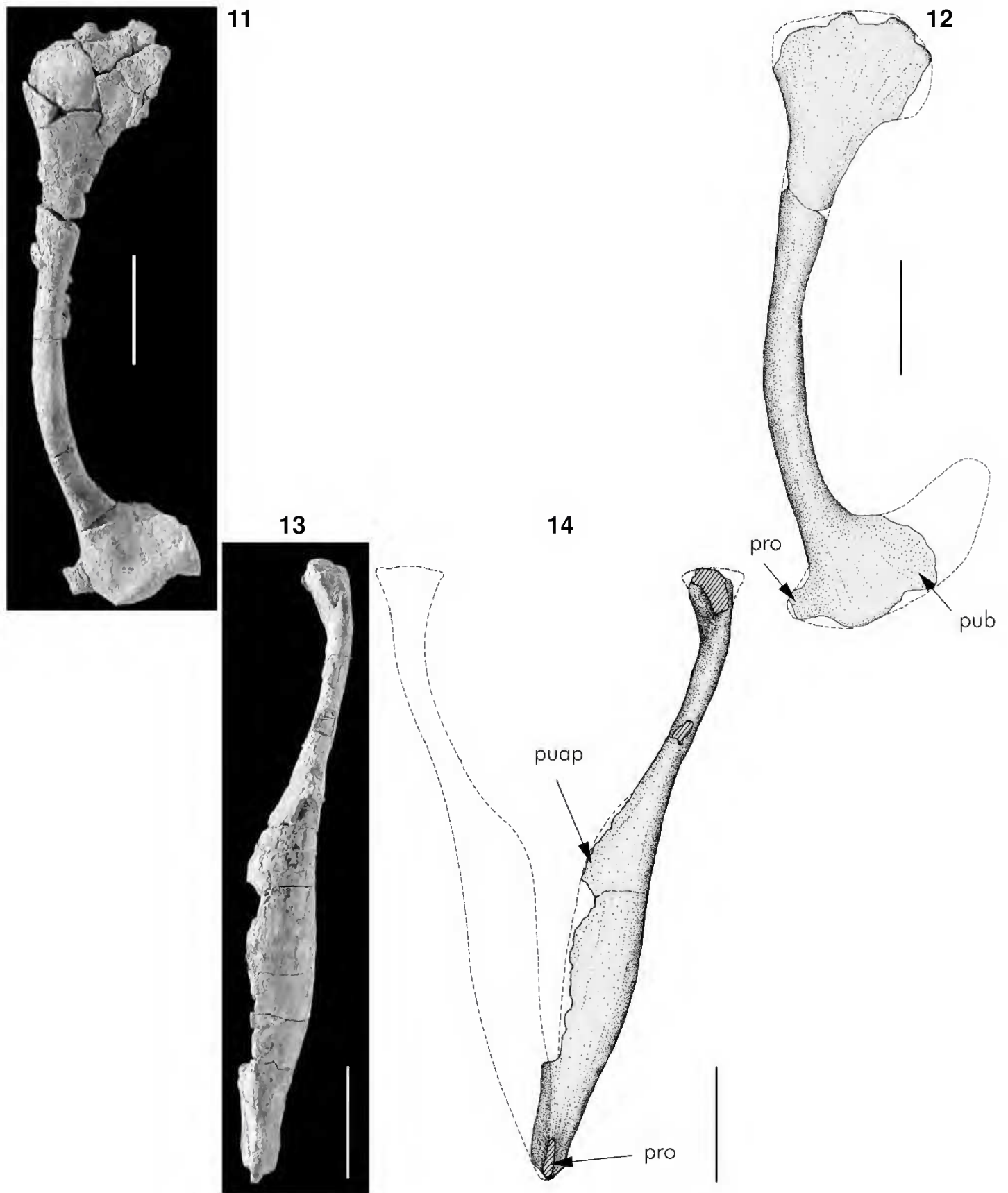
Only the posterior portion of the right ilium (MUCPv-409) was found (length of preserved portion: 103mm), including the posterior part of the acetabulum (Figs.22-31). In dorsal view, the dorsal margin of the preserved part is sigmoid, with the posterior end displaced laterally (Figs.24-25). The postacetabular blade forms a thin lamina of bone that shows a strong lateral concavity corresponding to a medial convexity. Overall it is short and acuminate, showing a marked inflection on the dorsal margin posterior to the acetabulum. The lateral surface is smooth. Close to the dorsal margin before the beginning of the inflected border of the postacetabular portion a rugose area is present; two distinct knob-like structures are present, possibly for muscle attachment. Some weakly grooves and ridges, likely for muscle scars, are also present at the most posterior end (on the lateral and medial surfaces). Ventrally, the brevis fossa is narrow and shallow. Medially a marked ridge forms the medial shelf of the brevis fossa that is directed posterodorsally running divergent from the ventral margin of the postacetabular blade. A rounded depression is present above the posterior part of the acetabulum. The preserved surface of the acetabulum forms a rugose surface that broadens posteriorly, ending in a thick posterior edge ("lip") that is part of the ischiadic peduncle.



Comparison of the proximal part of the left humerus of *Unenlagia comahuensis* (MCF PVPH 78 - left) and *Unenlagia paynemili* n.sp. (MUCPv-349 - right) – fig.9- picture, fig.10- drawing. (dpc) delto pectoral crest, (itub) internal tuberosity, (rid) ridge. Scale bars = 50mm.

Comparing the preserved part of the ilium with other coelurosaurs, *Unenlagia paynemili* n.sp. shows the postacetabular part of the ilium acuminate, a feature considered synapomorphic of the Maniraptora (NORELL, CLARK & MAKOVICKY, 2001) that contrasts to the more square outline observed in other theropods such as *Sinraptor* (CURRIE & ZHAO, 1993). The brevis fossa is shelf-like, a common feature within Maniraptora. Among coelurosaurs, *Unenlagia paynemili* n.sp. shares one feature, at the ilium, with *Unenlagia*

*comahuensis* – the marked inflection of the dorsal margin of the postacetabular blade that is here considered a diagnostic feature of the genus *Unenlagia*. The main differences between those species are the more rounded (and less) acuminate posterior edge and the shallower brevis fossa of *Unenlagia paynemili* n.sp. that also has a narrower and more open posterior portion of the acetabulum. Furthermore *Unenlagia comahuensis* shows a well developed ridge dividing the brevis fossa that is absent in *Unenlagia paynemili* n.sp.



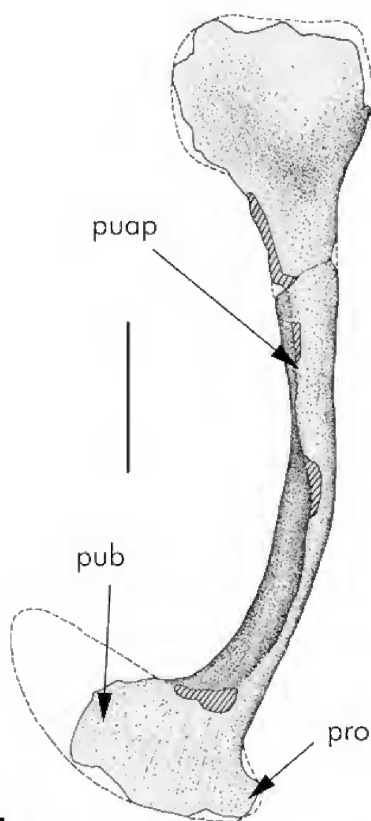
*Unenlagia paynemili* n. sp., left pubis (MUCPv-349) – fig. 11- picture, lateral view; fig. 12- drawing, lateral view; fig. 13- picture, anterior view; fig. 14- drawing, anterior view. (pro) bone projection, (puap) pubic apron, (pub) pubic boot. Scale bars = 50mm.



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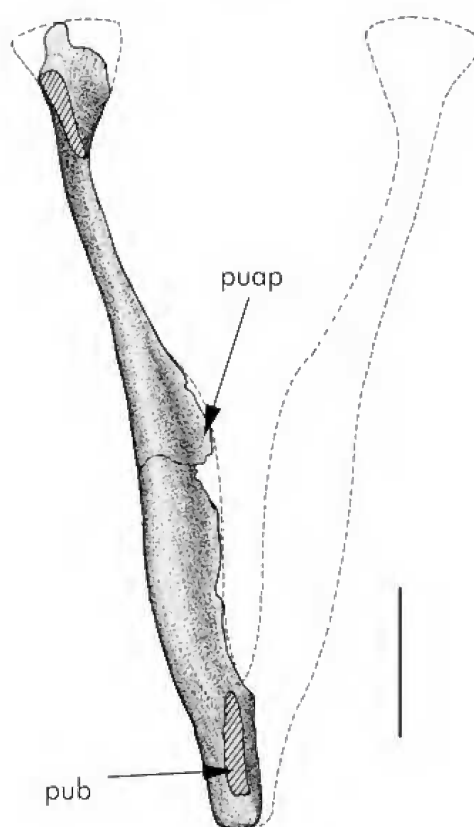
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*Unenlagia paynemili* n.sp., left pubis (MUCPv-349) – fig.15- picture, medial view; fig.16- drawing, medial view; fig.17- picture, posterior view; fig.18- drawing, posterior view. (pro) bone projection, (puap) pubic apron; (pub) pubic boot. Scale bars = 50mm.

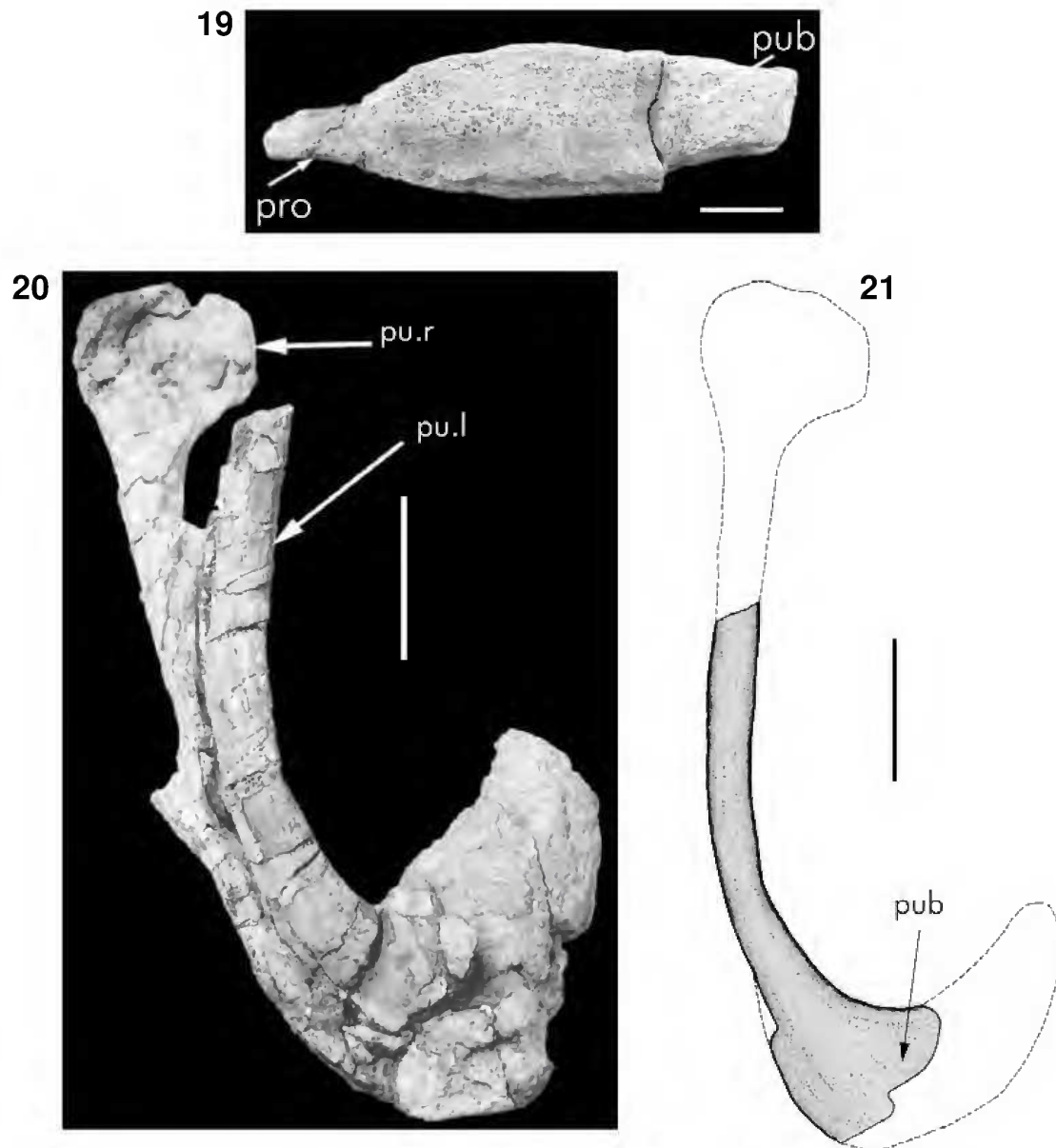
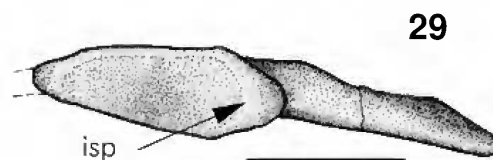
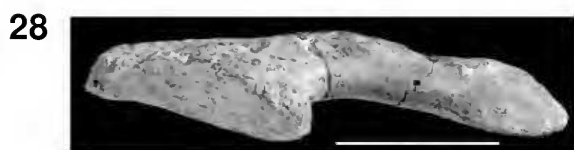
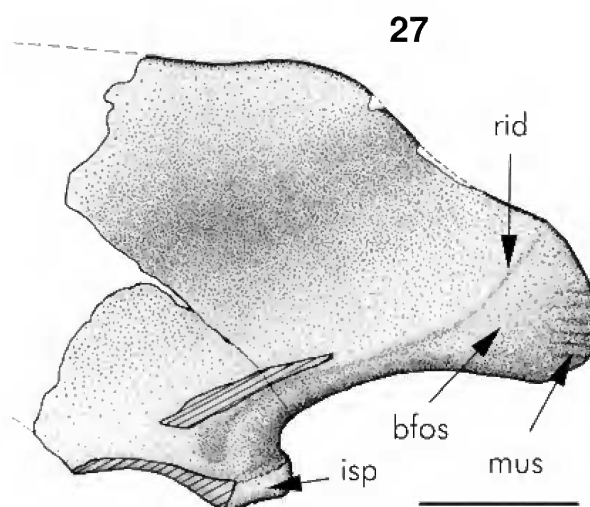
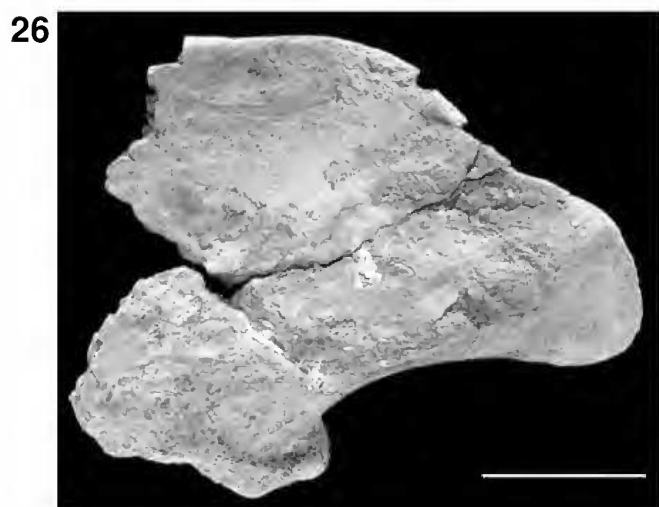
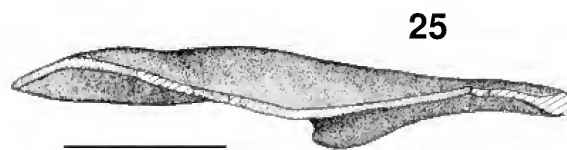
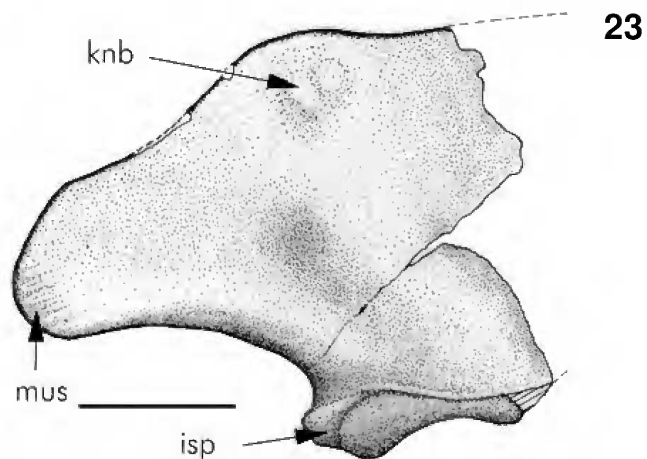
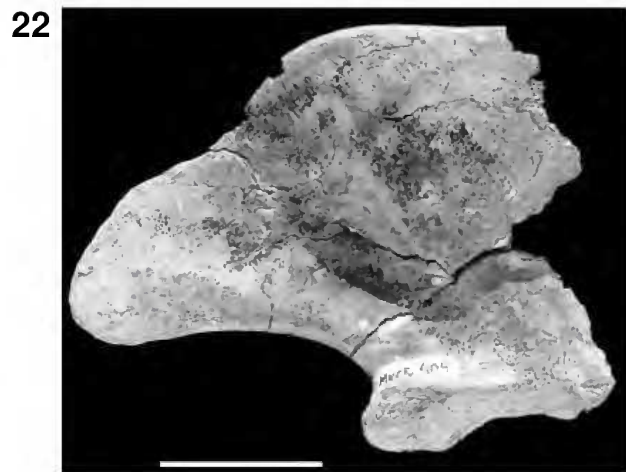


Fig.19- *Unenlagia paynemili* n.sp., picture of the distal part of the left pubis (MUCPv-349) showing the pubic boot and the anterior projection. Scale bar = 10mm. *Unenlagia comahuensis* (MCF PVPH 78) – fig.20- picture of the pubia, fig.21- drawing of the left pubis (MUCPv-349) in lateral view. Scale bar = 50mm. (pro) bone projection, (pub) pubic boot, (pu.l) left pubis, (pu.r) right pubis.

Only one dorsal vertebra (MUCPv- 416) was found. It shows the centrum and part of the neural arch, lacking the neural spine and most of the zygapophyses (Figs.32-35). Neural arch and the centrum are fused. One deep lateral pit on the basal portion of the neural spine is present on each side (Figs.34-35). Other more laterally placed openings (two on the right and one of the left side) are also observed and were possibly situated at the ventral base of the transverse processes that are broken in this specimen (Figs.32-33). The basal part of the

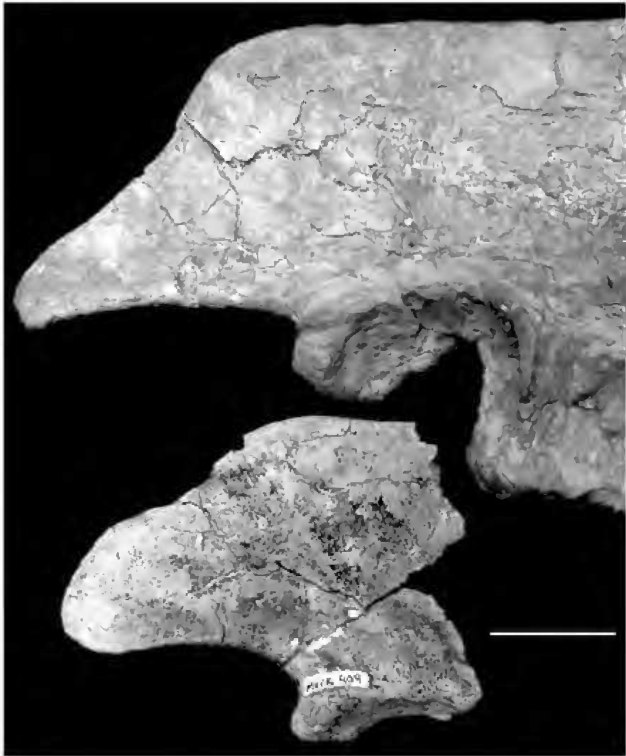
postzygapophyses is preserved and indicates that they are placed lateral to the neural canal and separated by a groove for the interspinous ligaments. Although present, hyposphenes are not sufficiently preserved to determine if they are separated, a feature present in *Unenlagia comahuensis* and in most Maniraptora (NORELL, CLARK & MAKOVICKY, 2001). The parapophyses are situated on the neural arch. The last one is not complete; although, they are clearly projected outward, a common feature present in dromeosaurids (and alvarezsaurids).



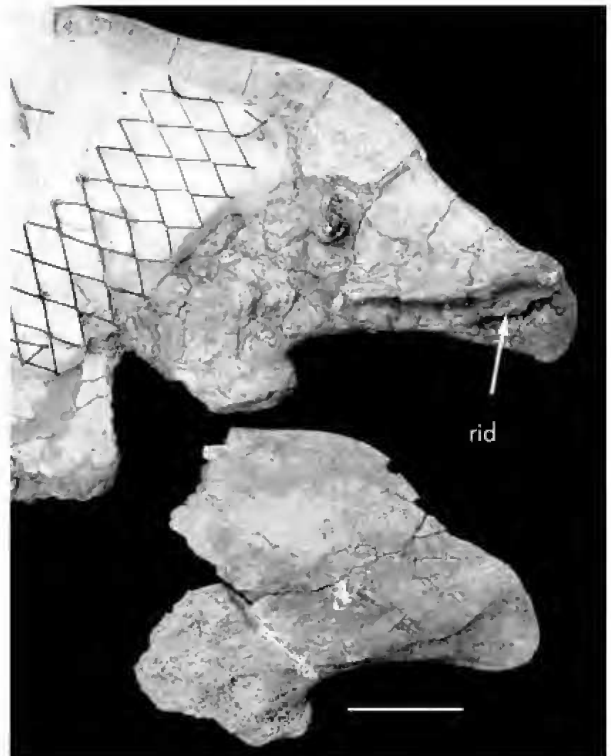
*Unenlagia paynemili* n.sp., right ilium (MUCPv-409) – fig.22- picture, lateral view; fig.23- drawing, lateral view; fig.24- picture, dorsal view; fig.25- drawing, dorsal view; fig.26- picture, medial view; fig.27- drawing, medial view; fig.28- picture, ventral view; fig.29- drawing, ventral view. (bfos) brevis fossa, (isp) ischiadic peduncle; (knb) knob-like protuberance; (mus) muscle scars, (rid) ridge. Scale bars = 30mm.



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Picture comparing the posterior part of the right ilium of *Unenlagia comahuensis* (MCF PVPH 78 - top) and *Unenlagia paynemili* n.sp. (MUCPv-409 - bottom) – fig.30- lateral view, fig.31- medial view. (rid) ridge. Scale bars = 30mm.

The centrum is amphiplatyan, with the anterior articulation surface rounded and the posterior surface slightly wider than higher. Close to the contact with the neural arch, one pleurocoel followed by a small depression is present on each side. A shallow groove followed by a small foramen is present on the ventral side of the centrum.

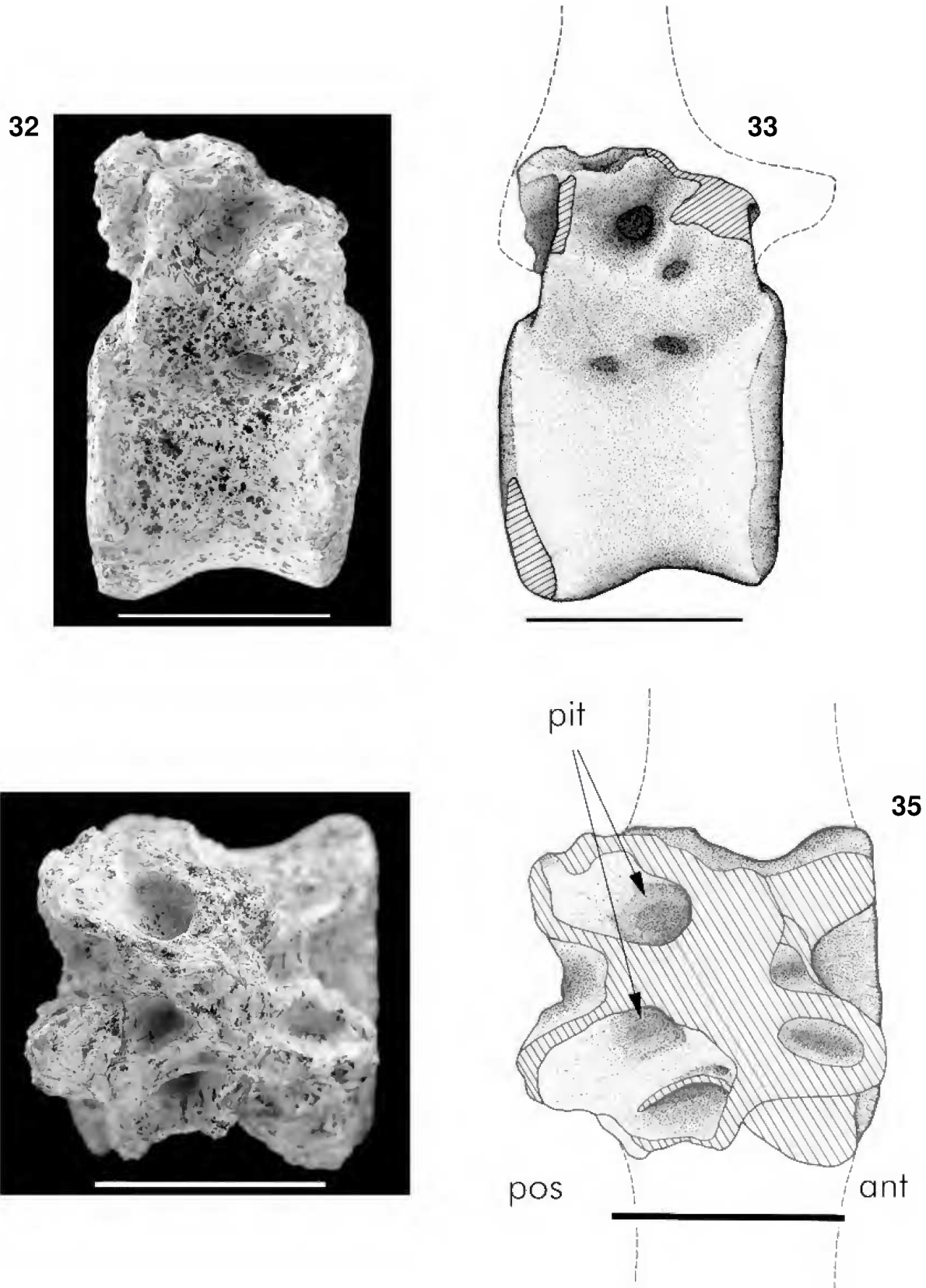
The most interesting feature of the MUCPv- 416 is the presence of a lateral pit close to the base of the neural spine, which has been reported in the posterior dorsals of *Unenlagia comahuensis* (NOVAS & PUERTA, 1997). Other dorsals of the holotype of this species, however, do not show this feature (pers. obs.)

A complete pedal phalanx (MUCPv-415) was also found in the same quarry and is tentatively referred to *Unenlagia paynemili* n.sp. (Figs.36-37). The specimen is complete and represents the first phalanx of the right digit I. The distal condyles are asymmetric and are separated by a marked groove. The lateral condyle shows a developed sub-circular fossa (possible for ligaments) while in the medial condyle this fossa is less developed. Proximally the articulation with the metatarsal is formed by two asymmetric surfaces separated by a blunt ridge, with the lateral one larger than the medial. Dorsally a bony ridge is positioned on the medial side. It

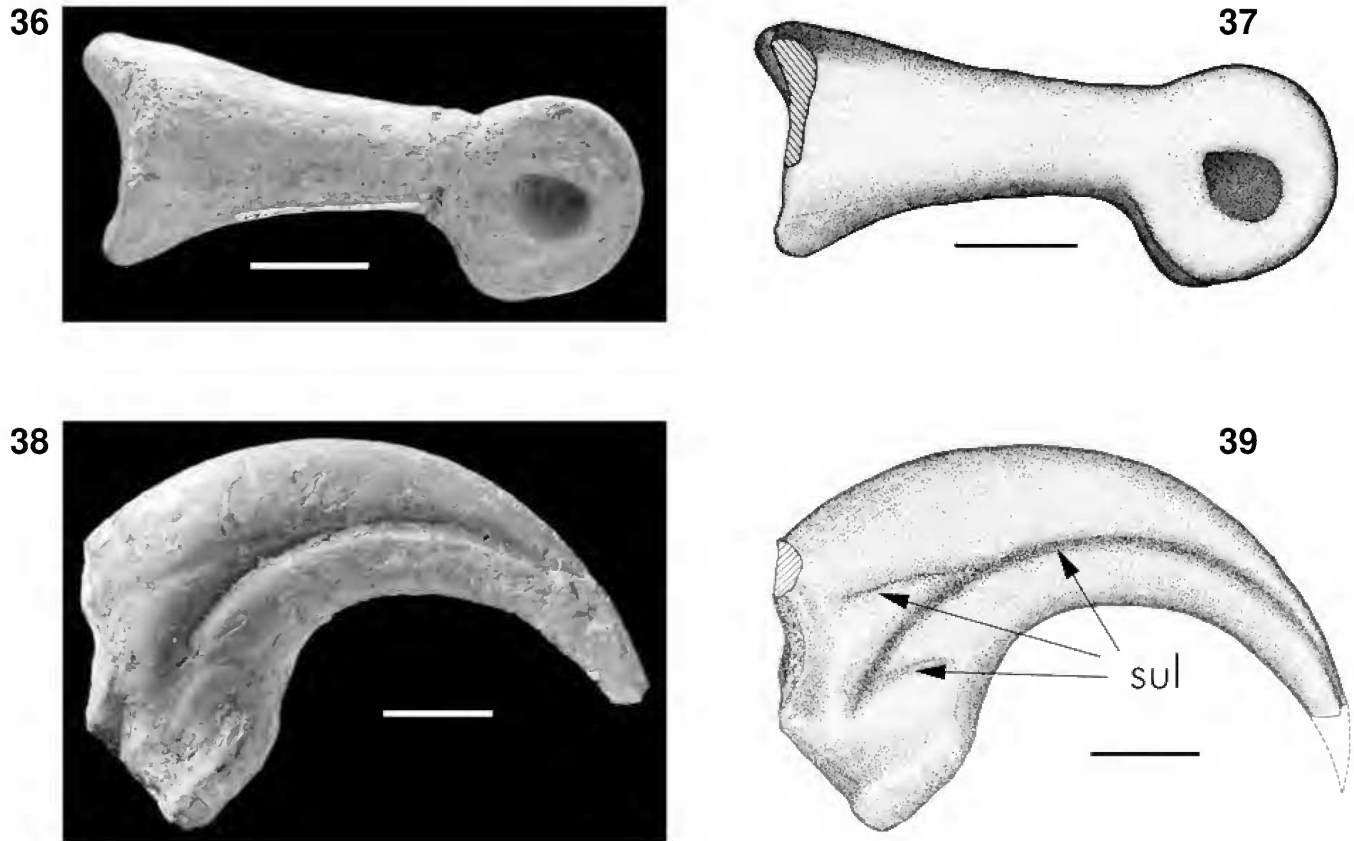
extends about one third of the total length of the phalanx, and it was likely the attachment surface for a muscle or ligament.

An ungueal phalanx (MUCPv-343) is also tentatively referred to *Unenlagia paynemili* n.sp. (Figs.38-39). It is strongly curved and laterally compressed, 65mm long on the dorsal border, and about 29mm high at the proximal end. On each side there is a groove that runs on the middle part of the claw, starting proximally close to the basal portion, reaching the dorsal margin close to the tip. Two additional parallel sulcus are present on one side. The upper sulcus runs from the proximal region, near the articular facets up to the middle groove. The lower sulcus starts at the base of the middle groove and reaches the ventral region of the claw anterior to the flexor tubercle. The ventral rim is lateroventrally rounded. It presents a flexor tubercle well developed placed below the articular facets, the latter being asymmetrical.

The lateral compression and the curvature of the *Unenlagia paynemili* n.sp. claw resemble that present in digit I of *Rahonavis* Forster, Sampson, Chiappe, & Krause, 1998. Although no foot is known from *Unenlagia comahuensis*, it should be noted that FORSTER *et al.* (1998) suggest that *Unenlagia comahuensis* should have had a similar claw to *Rahonavis*.



*Unenlagia paynemili* n.sp., dorsal vertebra (MUCPv-416) – fig.32- picture, right lateral view; fig.33- drawing, right lateral view; fig.34- picture, dorsal view; fig.35- drawing, dorsal view. (ant) anterior, (pit) lateral pit, (pos) posterior. Scale bars = 30mm.



Pedal phalanx (MUCPv-415), which is tentatively referred to *Unenlagia paynemili* n.sp. – fig.36- picture, fig.37- drawing, lateral view. Ungueal (MUCPv-343), which is tentatively referred to *Unenlagia paynemili* n.sp. – fig.38- picture, fig.39- drawing, lateral view. (sul) sulcus. Scale bars = 10mm.

## DISCUSSION

The dinosaur material collected from the Futalognko site includes articulated and isolated material. As common in paleontology, it is always difficult to associate isolated bones to one taxon, which is also the case of the material of *Unenlagia paynemili* n.sp. However, each of the main bones – the humerus, pubis, ilium and vertebra shows features attributed to *Unenlagia* (NOVAS & PUERTA, 1997). Based on the proportions and proximity in the quarry, the humerus and pubis are regarded as belonging to the same individual. Although the ilium might also belong to the same individual as the former, its position in the quarry lead us to cautiously regard it as belonging to a different animal of the same species. The dorsal vertebra definitively belongs to another much larger individual, but the presence of deep lateral pits in the base of the neural spines suggests that it belongs to an *Unenlagia*-type taxon and is therefore referred to *Unenlagia paynemili* n.sp.

In order to assess the phylogenetic position of the Barreal taxon, we used the comprehensive phylogenetic analysis of coelurosaurian relationship presented by NORELL, CLARK & MAKOVICKY (2001), consisting of 44 taxa (including *Unenlagia comahuensis*) and 205 characters. They used the algorithm NONA v. 1.9 through the WinClada interface and obtained 1065 equally parsimonious trees with a length of 554 steps, consistency index (CI) of 0.45 and a retention index of (RI) 0.73. We used the same data set and run it through PAUP 4.0b10 for Microsoft Windows, using the general heuristic search option (SWOFFORD, 2000). Characters were given equal weight and 11 were ordered, *Allosaurus* and *Sinraptor* were used as outgroups, following NORELL, CLARK & MAKOVICKY (2001). The consensus tree was further analyzed by MacClade 3.04 (MADDISON & MADDISON, 1992).

Differing from the previous study, PAUP encountered a much larger number of equally parsimonious trees (170.100; CI: 0.4554; RI:



0.7150) with a shorter length of 549 steps. The consensus tree also differs from the one published by NORELL, CLARK & MAKOVICKY (2001), by recovering a monophyletic Dromaeosauridae (including *Unenlagia comahuensis*) in sister group relationship with the Avialae (compare figures 40 and 41). Within Dromaeosauridae, PAUP recovered a trichotomy formed by *Unenlagia*, *Sinornithosaurus* and all other dromaeosaurids (which in the previous study formed a polytomy). Furthermore, PAUP resolved the relationship between Troodontidae, with *Sinornithoides* followed stepwise by *Byronosaurus*, *Troodon* and *Saurornithoides*.

The next step was to include the information available for *Unenlagia paynemili* n.sp. using the same data matrix and run it through PAUP. Only 10 characters could be scored for the new species (141/ 162/ 180: state 0; 105-106/ 160/ 176-178: state 1; 179: state 2), all remaining are unknown (1-104/ 107-140/ 142-159/ 161/ 163-175/ 181-205: ?). We also changed character 179, concerning the pubic shaft, which according to NORELL, CLARK & MAKOVICKY (2001) could vary from being straight (state 0) or curved anteriorly (state 1). The direct observation of the holotype of *Unenlagia comahuensis*, as well as the Barreal specimen, leads us to include a third state: distal end of pubis curved posteriorly (state 2). This modified data set was run through PAUP and obtained the same number of equally parsimonious trees which were expectedly one step longer (550 steps; CI: 0.4564; RI: 0.7158). The topology of the tree did not change, and differed only by showing a monophyletic grouping formed by *Unenlagia comahuensis* and the Barreal specimen (Fig.41). Based on the comparisons and phylogenetic analysis, we opted to consider the Barreal specimen congeneric with *Unenlagia comahuensis*, proposing the new species *Unenlagia paynemili* n.sp. Although it is quite possible that a generic differentiation might be applied in the future for the Barreal taxon, we prefer to wait until more complete and articulated material comes to light. According to the hypothesis of coelurosaurian relationships published by NORELL, CLARK & MAKOVICKY (2001), *Unenlagia paynemili* n.sp. presents two maniraptoran synapomorphies: the acuminate postacetabular ala of the ilium and vertical placed pubis (proximal part). The new Barreal taxon also shows a synapomorphy that unites all maniraptoran except *Ornitholestes*: the brevis fossa shelf-like. It further has a comparatively

small anterior projection of the pubic boot also absent or slightly projected in Avialae and Dromaeosauridae opposed to the well anterior projection known in most other theropods (e.g., *Allosaurus*, *Deinonychus antirrhopus*). *Unenlagia paynemili* n.sp. does not have at least one synapomorphy of the Avialae: reduced pubic apron. Furthermore it shares one synapomorphic feature with *Unenlagia comahuensis*: the posteriorly oriented distal end of the pubis.

Among the diagnostic features of *Unenlagia comahuensis*, NOVAS & PUERTA (1997) point out the presence of lateral pits at the base of the neural spines of the posterior dorsals and anterior sacrals and the inflected margin of postacetabular iliac blade. Those features are present in the referred specimens of *Unenlagia paynemili* n.sp. and might be considered two additional synapomorphies uniting those taxa. It should be noted, however, that the two additional dorsal vertebrae of the holotype of *Unenlagia comahuensis* lack lateral pits. The main differences between *Unenlagia comahuensis* and the new Barreal taxon is the different angle of the distal margin of the deltopectoral crest, the more rounded posterior edge of the ilium and the projection on the anterior part of the pubis. Furthermore the postacetabular portion of the ilium of *Unenlagia paynemili* n.sp. has a shallower brevis shelf with a smooth surface lacking the ridge present in *Unenlagia comahuensis*.

## CONCLUSIONS

The new Barreales lake species shares one synapomorphy with *Unenlagia comahuensis*: the particular posterior inclination of the distal end of the pubis. One more character is shared by those taxa and is regarded as a potential synapomorphy of *Unenlagia*: the inflected dorsal margin of the postacetabular iliac blade. Although the dorsal vertebra of the Barreal species also shows the lateral pits at the base of the neural spine observed in *Unenlagia comahuensis* (NOVAS & PUERTA, 1997), this feature is absent in the additional two dorsal vertebrae of the type material and has to be seen with caution. Although the Barreales lake material possibly represents a new genus, we regard classify this species within the genus *Unenlagia* until more material allowing a better characterization is found. The several observed anatomical differences, however, lead us to propose a new species, *Unenlagia paynemili* n.sp.

The phylogenetic position of *Unenlagia* is disputed

with some authors regarding this taxon in sister group relationships with the Avialae (NOVAS & PUERTA, 1997) member of the Avialae (FORSTER *et al.*, 1998) or a dromeosaurid not closely related to Avialae (NORELL & MAKOVICKY, 1999; NORELL, CLARK & MAKOVICKY, 2001). Unfortunately the incomplete nature of the *Unenlagia paynemili* n.sp. does not resolve this dispute. Since we used the data basis of NORELL, CLARK & MAKOVICKY (2001), we end up as having both species of *Unenlagia* as members of the Dromeosauridae (Fig.41). Although

the analysis of the coelurosaurian phylogenetic hypothesis published by NORELL, CLARK & MAKOVICKY (2001) is not the purpose of the paper, the fact that PAUP produced different results than NONA, particularly recovering shorter and more resolved parsimonious trees is somewhat intriguing and should be object of further studies.

In any case, the discovery of this new species of *Unenlagia* indicates a higher diversity of those enigmatic *Unenlagia*-type maniraptorans.

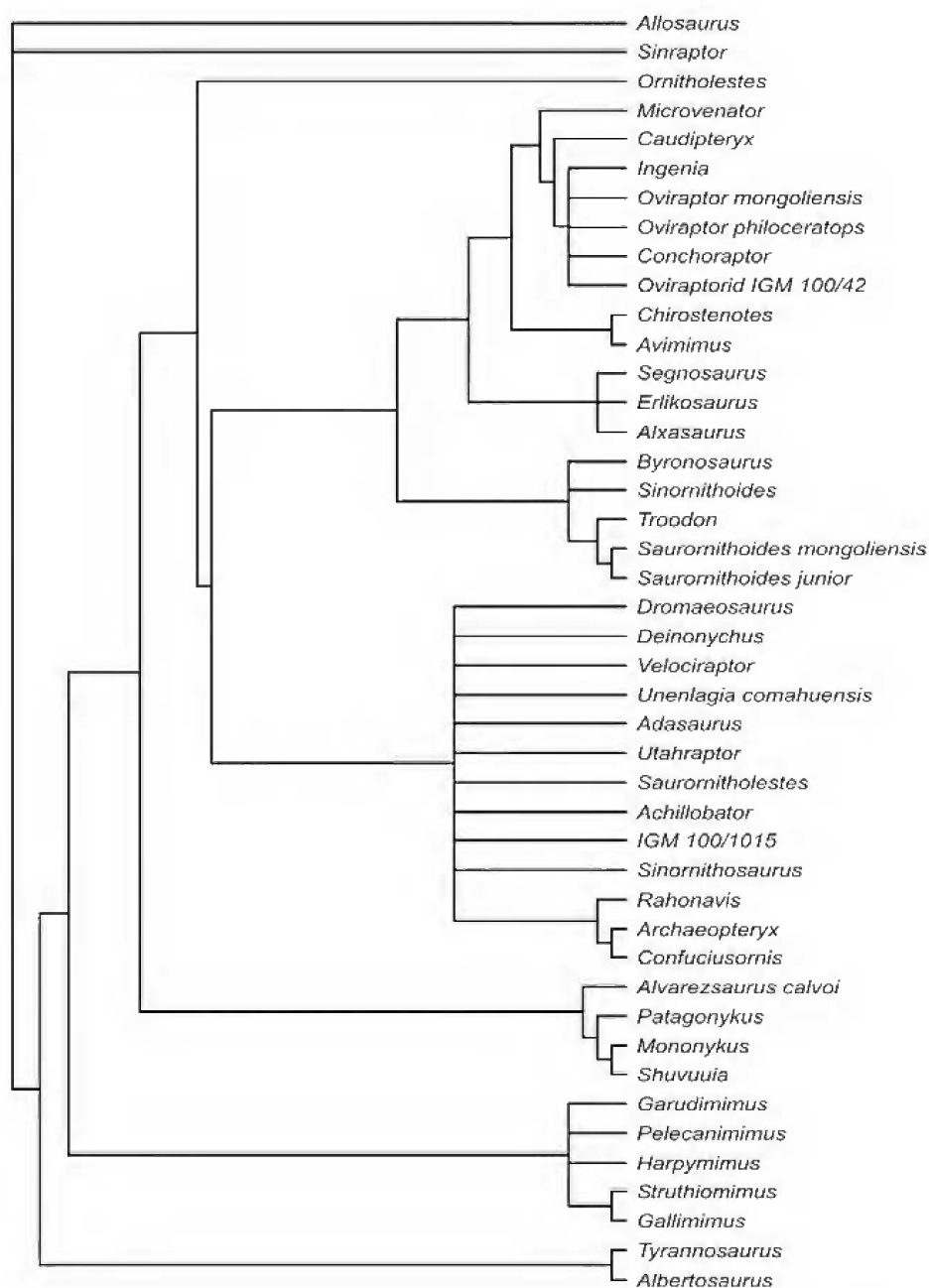


Fig.40- Strict consensus cladogram published by NORELL, CLARK & MAKOVICKY (2001).

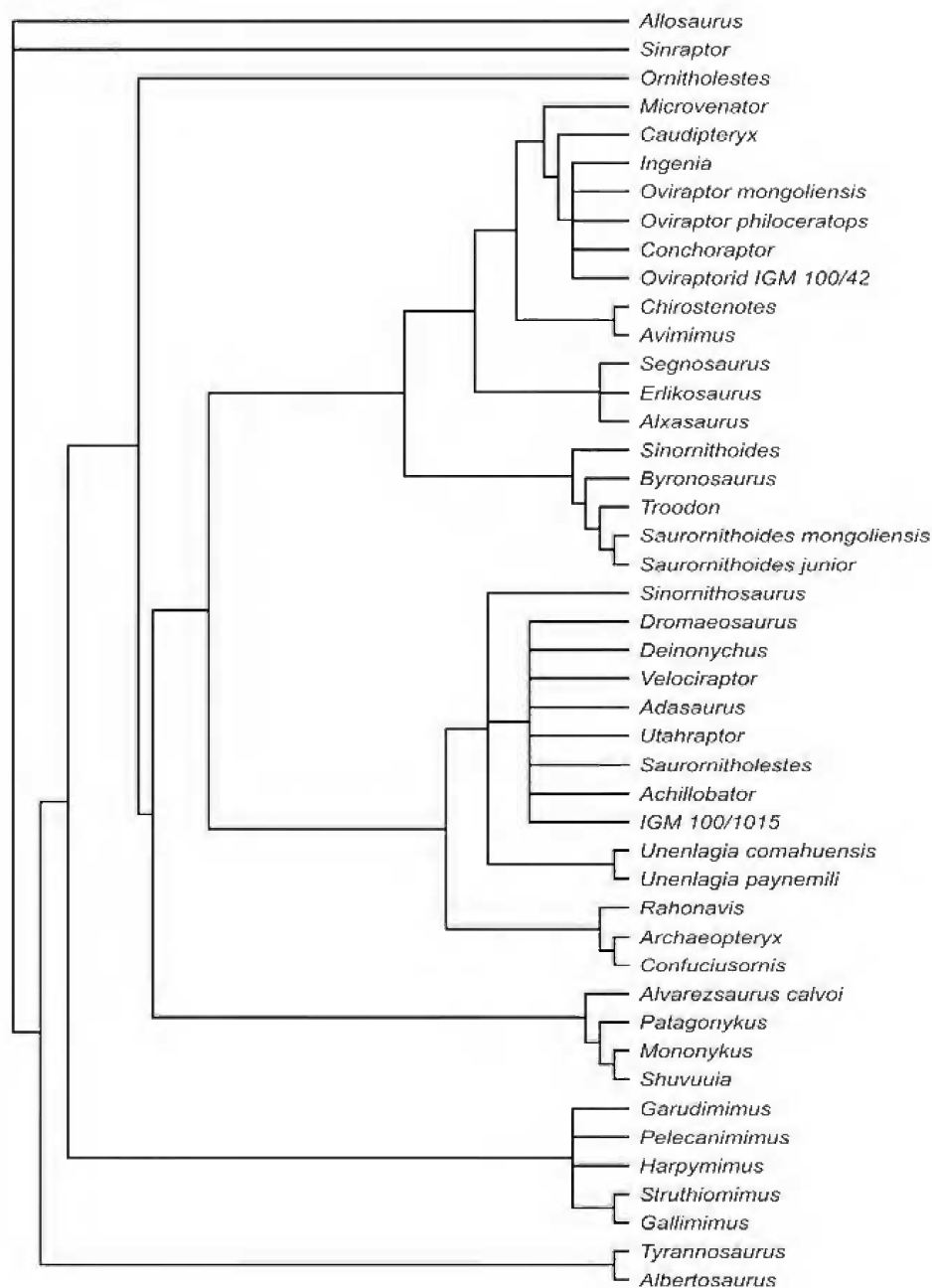


Fig.41- Strict consensus cladogram based on the data set of NORELL, CLARK & MAKOVICKY (2001) run through PAUP 4.0b10, including the *Unenlagia paynemili* n.sp. See text for details.

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## LITERATURE CITED

- BARSBOLD, R. & OSMÓLSKA, H., 1990. Ornithomimosauria. In: WEISHAMPEL, D.B.; DODSON, P. & OSMÓLSKA, H. (Eds.) **The Dinosauria**, Berkeley, p.225-244.
- BARSBOLD, R.; MARYANSKA, T. & OSMÓLSKA, H., 1990. Oviraptorosauria. In: WEISHAMPEL, D.B.; DODSON, P. & OSMÓLSKA, H. (Eds.) **The Dinosauria**, Berkeley, p.249- 258.
- BONAPARTE, J.F.; NOVAS, F.E. & CORIA, R.A., 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly build carnosaur from the middle Cretaceous of Patagonia. **Contributions Science, Natural History Museum of Los Angeles County**, Los Angeles, **416**:1-42.
- BROCHU, C.A., 2003. Osteology of *Tyrannosaurus rex*: Insights from a Nearly Complete Skeleton and High-Resolution Computed Tomographic Analysis of the Skull. **Journal of Vertebrate Paleontology**, Illinois, **22**(4):1-138.
- CALVO, J.O., 1991. Huellas Fósiles de dinosaurios en la Formación Río Limay (Albiano-Cenomaniano) Picún Leufú. Provincia del Neuquén. Argentina. (Ornithischia-Saurischia: Saurópoda-Terópoda) **Ameghiniana**, Buenos Aires, **28**(3-4):241-258.
- CALVO, J.O.; PORFIRI, J. & KELLNER, A.W.A., 2003. A close relative of *Unenlagia comahuensis* (Theropoda, Maniraptora) from the Upper Cretaceous of Neuquén, Patagonia, Argentina. In: **Boletim de Resumos, 18. Congresso Brasileiro de Paleontologia**, Brasília: Universidade de Brasília, p.82-83.
- CALVO, J.O.; PORFIRI, J.; VERALLI, C. & NOVAS, F., 2002a. *Megaraptor namunhuaiquii* (Novas, 1998), a new light about its phylogenetic relationships. In: VARGAS, A.; YÁNEZ, J.V. & RUBILAR, D.R. (Eds.), Sociedad Paleontológica de Chile. **Primer Congreso Latinoamericano de Paleontología de Vertebrados**, Santiago do Chile, p.20.
- CALVO, J.O.; PORFIRI, J.; VERALLI, C. & POBLETE, F., 2001. One of the largest titanosaurid sauropods ever found, Upper Cretaceous, Neuquén, Patagonia, Argentina. **61 Annual Meeting Society of Vertebrate Paleontology**, Illinois, **21**(3):37A.
- CALVO, J.O.; PORFIRI, J.; VERALLI, C.; POBLETE, F. & KELLNER, A.W.A., 2002b. Futalognko Paleontological Site, one of the most amazing Continental Cretaceous Environments of Patagonia, Argentina. In: VARGAS, A.; YÁNEZ & RUBILAR, D.R. (Eds.), Sociedad Paleontológica de Chile. **Primer Congreso Latinoamericano de Paleontología de Vertebrados**, Santiago do Chile, p.19.
- CALVO, J.O. & SALGADO, L., 1995. *Rebbachisaurus tessonei* sp.nov. a new sauropod of the Albian-Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. **Gaia**, Lisboa, **11**:13-33.
- CAZAU, L.B. & ULIANA, M.A., 1973. El Cretácico superior continental de la Cuenca Neuquina. **V Congreso Geológico Argentino**, Buenos Aires, Actas **3**:131-163.
- CURRIE, P. & ZHAO, X., 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. **Canadian Journal of Earth Sciences**, Ottawa, **30**(10-11):2037-2081.
- FORSTER, C.A.; SAMPSON, S.D.; CHIAPPE, L.M. & KRAUSE, D.W., 1998. The theropod Ancestry of Birds: New evidence from the Late Cretaceous of Madagascar. **Science**, Washington, **279**:1915-1919.
- GALLO, V.; CALVO, J.O. & KELLNER, A.W.A., 2003. First occurrence of a teleostean fish in the Portezuelo Formation (Upper Cretaceous), Neuquén Group, Patagonia - Argentina. Universidade do Estado do Rio de Janeiro, **III Simpósio Brasileiro de Paleontologia de Vertebrados**, Rio de Janeiro, p.29.
- KELLNER, A.W.A. & CAMPOS, D.A., 2002. On a Theropod Dinosaur (Abelisauria) from the Continental Cretaceous of Brazil. **Arquivos do Museu Nacional**, Rio de Janeiro, **60**(3):163-170.
- KELLNER, A.W.A.; CALVO, J.O.; SAYÃO, J.M. & PORFIRI, J., 2004. First Pterosaur from the Portezuelo Formation, Neuquén Group, Patagonia, Argentina. **IV Simpósio Brasileiro de Paleontologia de Vertebrados**. Rio Claro, p.29-30.
- LEANZA, H.A., 1999. The Jurassic and Cretaceous Terrestrial Beds from Southern Neuquén Basin, Argentina. **Miscelanea**, Tucumán, **4**:1-30.
- LEANZA, H.A. & HUGO, C.A., 2001. Cretaceous red beds from southern Neuquén Basin (Argentina): age, distribution and stratigraphic discontinuities. In: Leanza, H.A. (Eds.) Asociación Paleontológica Argentina. **VII International Symposium on Mesozoic Terrestrial Ecosystems**, Buenos Aires, **7**:117-122.
- LEGARRETA, L. & GULISANO, C., 1989. Análisis estratigráfico secuencial de la Cuenca Neuquina (Triásico superior-Terciario inferior). In: CHEBLI, G. & SPALLETTI, L. (Eds.) Cuencas Sedimentarias Argentinas. **Serie Correlación Geológica**. Universidad Nacional de Tucumán, Tucumán, **6**:221-243.
- MADDISON, W.P. & MADDISON, N.D.R., 1992. MacClade, 3.04. Sinauer Associates, Inc. Sunderland, Massachusetts.
- MARTILL, D.; FREY, E.; SUES, H.D. & CRUIKSHANK, A., 2000. Skeletal remains of a small theropod dinosaur with associated soft structures from the Lower Cretaceous Santana Formation of northeastern Brazil. **Canadian Journal of Earth Sciences**, Canada, **37**:891-900.
- NORELL, M.A. & MAKOVICKY, P.J., 1999. Important Features of the Dromaeosaurid Skeleton II: Information from Newly Collected Specimens of *Velociraptor mongoliensis*. **American Museum Novitates**, New York, **3282**:1-45.

- NORELL, M.A.; CLARK, J.M. & MAKOVICKY, P.J., 2001. Phylogenetic relationships among coelurosaurian theropods. **New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom**. Peabody Museum of Natural History, New Haven, 49-67.
- NOVAS, F.E., 1996. Alvarezsauridae, Cretaceous basal birds from Patagonia and Mongolia. Proceedings of the Gondwanan Dinosaur Symposium. **Memoirs Queensland Museum**, Brisbane, **39**(3):675-702.
- NOVAS, F., 1998. *Megaraptor namunhuaiquii*, Gen. et sp.nov., a large-clawed, late Cretaceous theropod from Patagonia. **Journal of Vertebrate Paleontology**, Illinois, **18**(1):4-9.
- NOVAS, F.E. & PUERTA, P., 1997. New evidence concerning avian origins from the late Cretaceous of Patagonia. **Nature**, London, **387**:390-392.
- OSBORN, H.F., 1905. *Tyrannosaurus* and other Cretaceous carnivorous dinosaur (second communication). **Bulletin of the American Museum of Natural History**, New York, **21**:259-265.
- OSTROM, J.H., 1969a. A new theropod dinosaur from the Lower Cretaceous of Montana. **Postilla**. Peabody Museum Natural History, New Haven, **128**:1-17.
- OSTROM, J.H., 1969b. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. **Peabody Museum Natural History**, New Haven, Bulletin **30**:1-165.
- PERLE, A.; NORELL, M. & CLARK, J., 1999. A new maniraptoran Theropod-*Achillobator giganteus* (Dromaeosauridae) from the Upper Cretaceous of Burkland, Mongolia. **National University of Mongolia**, Mongolia, 1-104.
- POBLETE, F. & CALVO, J., 2003. Upper Turonian Dromaeosaurid teeth from Futalogno quarry, Barreales Lake, Neuquén, Patagonia, Argentina. **XIX Jornadas Argentinas de Paleontología de Vertebrados**, Buenos Aires p.24.
- PORFIRI, J. & CALVO, J.O., 2002. A new record of an ornithomimid dinosaur from the Upper Cretaceous of Neuquén, Patagonia, Argentina. In: VARGAS, A.; YÁNEZ, J.V. & RUBILAR, D.R. (Eds.), Sociedad Paleontológica de Chile. **Primer Congreso Latinoamericano de Paleontología de Vertebrados**. Santiago do Chile, p.45.
- PORFIRI, J.D. & CALVO, J.O., 2003. "Megaraptores" en Lago Barreales, Neuquén, Patagonia. **Reunión Anual de Comunicaciones de la Asociación Paleontológica Argentina y Simposio de Tafonomía y Paleoecología**. Santa Rosa, La Pampa. p.17.
- PRÁMPARO, M.B.; PASSALIA, M.G.; HEREDIA, S.; & CALVO, J.O., 2003. Hallazgo de una macroflora en el cretácico superior del Grupo Neuquén, Lago Barreales, Neuquén. **Reunión Anual de Comunicaciones de la Asociación Paleontológica Argentina y Simposio de Tafonomía y Paleoecología**. Santa Rosa, La Pampa. p.18.
- SÁNCHEZ, M.; CARDOZO, J.; HEREDIA, S. & CALVO, J. 2003. Sedimentología de la Formación Portezuelo (Grupo Neuquén), Cretácico Superior, en lago Los Barreales, Provincia del Neuquén. **2das. Jornadas Regionales en Ciencias de la Tierra**. San Juan. Actas, p.32.
- SWOFFORD, D.L., 2000. PAUP: Phylogenetic Analysis Using Parsimony. Version 4,0B10. Sinauer Associates. Inc. Sunderland, Massachusetts.
- ULIANA, M.A. & DELLAPE, D., 1981. Estratigrafía y evolución paleoambiental de la Sucesión Maastrichtiano-Eoterciaria del engolfamiento Neuquino (Patagonia Septentrional). **VIII Congreso Geológico Argentino**, San Luis. Actas **3**:673-711.
- VERALLI, C. & CALVO, J.O., 2003. New findings of carcharodontosaurid teeth (Upper Turonian) on Futalogno quarry, North Barreales Lake, Neuquén, Argentina. **XIX Jornadas Argentinas de Paleontología de Vertebrados**, Buenos Aires, p.31.
- WELLNHOFER, P., 1974. Das Funfte Skelettexemplar von *Archaeopteryx*. **Paleontographica**, Stuttgart, **147**(A):169-216.
- WELLNHOFER, P., 1993. Das siebte Exemplar von *Archaeopteryx* aus den Solnhofener Schichten. **Archaeopteryx**, Eichstätt, **11**:1-48.